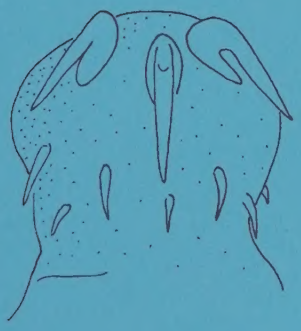
NOAA Technical Report NMFS 135

May 1998

Marine Flora and Fauna of the Eastern United States

Acanthocephala

Omar M. Amin



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Foreward

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Marine Flora and Fauna of the Eastern United States
Acanthocephala

OMAR M. AMIN

Institute of Parasitic Diseases
P.O. Box 28372, Tempe, Arizona 85285-8372 and
Department of Zoology
Arizona State University
Tempe, Arizona 85287-1501

ABSTRACT

The phylum Acanthocephala (intestinal worm parasites of vertebrates) of the Atlantic coast of the United States comprises 43 species and 20 genera belonging to three orders: Echinorhynchida, Neoechinorhynchida, and Polymorphida. Adults are exclusively intestinal parasites of vertebrates. This study includes those species found in vertebrates of marine and estuarine environments along the North American Atlantic coast between Maine and Texas. Species that can be found within that geographical range and those that typically infect freshwater fishes but that are occasionally present in marine or estuarine hosts are also included. The taxonomy, anatomy, natural history, and ecology of the phylum Acanthocephala are discussed, and an illustrated key to the genera is presented. Techniques, an annotated systematic treatment of all 43 species, and a systematic index are included. No systematic decisions will be made at this time, but areas where such decisions are pending will be indicated and discussed for future reports.

Introduction

All worms of the relatively small phylum Acanthocephala (= spiny-headed) are, as adults, parasitic in the intestines of all vertebrate groups.

They are pseudocoelomates with bilateral symmetry, have simplified anatomical structures, and all have similar reproductive processes and life cycles. Their parasitic adaptations to marine, freshwater, and terrestrial vertebrates render them much more versatile than their anatomical homogens may suggest. These adaptations include reduction of the muscular, nervous, circulatory, and excretory systems, and complete loss of the digestive system. Close phylogenetic relationships with other invertebrate phyla are not evident. Acanthocephalans bear superficial similarities to the nematodes, and some anatomical similarities to the cestodes can be demonstrated. Most genera and species occur in fishes, particularly freshwater fishes. "The absence of acanthocephalan parasites in elasmobranchs, their relatively small numbers in marine teleosts, and their extensive speciation in freshwater teleosts suggest a freshwater parasitic origin after the separation of elasmobranchs from their ancestral freshwater stock" (Amin, 1982b).

Taxonomy

The presently accepted system for classification of the Acanthocephala is that of Amin (1985a, 1987a) which was previously outlined by Amin (1982a). That system, for the most part, is based on the concepts proposed by Meyer (1931, 1932, 1933), modified by Van Cleave (1936), and expanded by Golvan (1959, 1960–1961, 1962, 1969) and Bullock (1969). The schemes of Petrochenko (1956, 1958) and Yamaguti (1963) are not recognized; see Amin (1985a, 1987a) for a detailed discussion.

The phylum Acanthocephala is divided into four classes:

1 Class Polyacanthocephala: includes only one monogeneric family in one order that parasitizes fish and crocodiles in South America and Africa.
2 Class Archiacanthocephala: comprises four orders that primarily infect predacious birds and mammals: order Apororhynchida (with one family, Apororhynchidae, and one genus parasitizing birds in Russia, North and South America, and Hawaii); order Gigantorhynchida (with one family, Gigantorhynchidae, and two genera that parasitize mam-

mals and birds around the world); order Moniliformida (with one family, Moniliformidae, and three genera that are widely distributed throughout the world in mammals and occasionally birds); order Oligacanthorhynchida (with one family, Oligacanthorhynchidae, and nine genera of worldwide distribution in birds, edentates, suids, insectivores, carnivores, simian primates, and marsupials).

3 Class Palaeacanthocephala: is the largest and most diversified class of acanthocephalans that parasitize fishes, amphibians, reptiles, birds, and mammals throughout the world. The class includes two orders: Echinorhynchida and Polymorphida. Members of the order Echinorhynchida are parasites of fishes, and occasionally amphibians and reptiles, and are placed in 10 families (Arhythmacanthidae with six genera in three subfamilies; Cavisomidae with 10 genera; Diplosentidae with four genera in two subfamilies; Echinorhynchidae with six genera in two subfamilies; Fessisentidae with one genus; Heteracanthocephalidae with four genera in two subfamilies; Hypoechinorhynchidae with two genera; Illiosentidae with 10 genera; Pomphorhynchidae with four genera; Rhadinorhynchidae with 22 genera in five subfamilies). Members of the order Polymorphida are parasites of amphibians, reptiles, birds, and mammals. The order includes three families (Centrorhynchidae with two genera; Plagiorhynchidae with nine genera in three subfamilies; and Polymorphidae with nine genera).

4 Class Eoacanthocephala: includes parasites of fishes and less frequently parasites of amphibians and reptiles. It consists of two orders: Order Gyracanthocephala (with eight genera in one family, Quadrigyridae, and two subfamilies) and order Neoechinorhynchida with three families (Dendronucleatidae with one genus; Neoechinorhynchidae with 18 genera in three subfamilies; and Tenuisentidae with two genera).

The acanthocephalan species treated in this manual are known from fishes, mammals, and birds that are naturally found in marine as well as estuarine habitats. Freshwater acanthocephalans that have been reported occasionally from fish hosts in marine or estuarine locations within the geographical range covered by this manual are also included. Marine acanthocephalans reported outside of this range, but that may prove to be present within it, are also discussed. A total of 43 species in 20 genera of acanthocephalans are treated in this manual in the following sections. The genera belong to three orders as follows:

Order Echinorhynchida: *Acanthocephalus* Koelreuther, 1771; *Dollfusentis* Golvan, 1969; *Echinorhynchus* Zoega in Müller, 1776; *Filisoma* Van Cleave, 1928; *Gorgorhynchoides* Cable and Linderoth, 1963; *Gorgorhynchus* Chandler, 1934; *Leptorhynchoides* Kostylev, 1924; *Pomphorhynchus* Monticelli, 1905; *Serrasentis* Van Cleave, 1923; *Tegorhynchus* Van Cleave, 1921.

Order Neoechinorhynchida: *Atactorhynchus* Chandler, 1935; *Floridosentis* Ward, 1953; *Neoechinorhynchus* Stiles and Hassall, 1905; *Paratenuisentis* Bullock and Samuel, 1975.

Order Polymorphida: *Andracantha* Schmidt, 1975; *Arhythmorhynchus* Lühe, 1911; *Bolbosoma* Porta, 1908; *Corynosoma* Lühe, 1904; *Polymorphus Southwellina* Witenberg, 1932.

Anatomy of Adults

Like cestodes, adult acanthocephalans are obligate intestinal parasites that lack a digestive system. They are dioecious and females are usually larger than males of the same species. The body consists of the proboscis, neck, and trunk. The **proboscis** may be short and stubby with few hooks or cylindrical with many hooks. Except for one order, Apororhynchida, the proboscis is armed with recurved sclerotized hooks and is retractable into a receptacle that houses the "brain" (cerebral ganglion). **Proboscis hooks** are often arranged in longitudinal rows and may vary in shape, size, and root structure anterioposteriorly or dorsoventrally. The growth pattern of proboscis hooks and the relationship of this growth pattern to acanthocephalan establishment and attachment to host intestinal mucosa have been studied in a few species (e.g. see Amin, 1986b, 1987c). Proboscis hooks are usually rooted, and these **roots** are often simple and directed posteriorly; many variations exist. An **apical organ** at the anterior tip of the proboscis of a few species, which may have a sensory or secretory function, has been described.

The **neck** is the unarmed area directly following the posteriormost circle of hooks on the proboscis. It may be practically nonexistent or very long, well-developed, and capable of of being enlarged into a bulb at some point in its length, as in the palaeacanthocephalan family Pomphorhynchidae. The **proboscis receptacle** may be single-walled (e.g. in Eoacanthocephala and some archiacanthophalans) or double-walled. The pattern of proboscis receptacle musculature is variable and may assume spiral or diagonal arrangement; see, for example, the archiacanthocephalan order Moniliformida. Some palaeacanthocephalans (e.g. family Fessisentidae) have a **nuclear pouch** at the posterior extremity of the proboscis receptacle,

The central structure of the nervous system is the "**brain**" (cerebral ganglion) which is invariably present within the proboscis receptacle at various levels in different families and genera. The ganglia are associated

with the peripheral nervous system which is more complex in male than female worms. The **genital** and **bursar ganglia** are found at the posterior end of males and are associated with reproductive activity. The sensory receptor system includes the **apical structure** which is located at the anterior tip of the proboscis of some acanthocephalans and may vary from a simple papilla to an extrudable depression surrounded by specialized cells and ducts. Sensory **support cells** and **sensory pits** also have been described from a few acanthocephalan species.

The **trunk** is usually cylindrical but may (rarely) be ribbonlike or have superficial annulations. It is often unarmed (spineless) but may be armed with spines of many shapes and sizes that are variously distributed. Most adults vary from a few mm to 1 or 2 cm in length. However, some oligacanthorhynchid archiacanthocephalans, e.g. *Macracanthorhynchus hirudinaceus* from pigs and *Oligacanthorhynchus longissimus* from aardvarks may reach 45 and 93 cm in length, respectively. Absorption of nutrients occurs through the **body wall** which contains a **lacunar** (circulatory) **system** with lateral longitudinal canals (in Palaeacanthocephala) or dorsoventral longitudinal canals (in other classes). The body wall contains **hypodermal nuclei** that may fragment in adults. **Giant nuclei**, at least in the genus *Neoechinorhynchus*, appear to be associated with the reproductive activity of worms (Amin and Vignieri, 1986a, 1986b; Amin and Gunset, 1992). The **tegument** of adult acanthocephalans includes the following layers from the surface: glycocalyx; outer limiting membrane; striped, vesicular, felt, and outer radial layers; inner membrane; and connective layer. A detailed discussion of the functional morphology of the various anatomical structures and organ systems of the Acanthocephala is presented by Miller and Dunagan (1985).

A pair of **lemnisci** originate at the base of the neck and are believed to have absorptive function comparable to that of the body wall. They may be equal or unequal in length, short or very long, nucleated or nonnucleated, and variously shaped.

Excretion and osmoregulation are accomplished by diffusion in all acanthocephalans, except in members of Oligacanthorhynchidae, which have two specialized **protonephridial organs**. Two types of protonephridia are known: dendritic or capsular saclike.

The **reproductive system** in both sexes is suspended in the body cavity by one or two long hollow **ligament sacs** that extend between the base of the proboscis receptacle to near the distal genital pore. The ligament sacs may or may not persist in adults. The **female reproductive system** consists of **gonads** from which **ovarian balls** develop and, after fertilization, produce **oocytes** and **eggs**. In a few precocious species, the ovarian balls may begin to develop in the last larval stage (the **cystacanth**) while still in the body cavity of the intermediate host (see Amin, 1982b). The **efferent duct** of the female system includes the **uterine bell**, **uterus**, and **vagina**. The anterior bell chamber opens posteriorly into the selector apparatus which allows the passage of only fertilized, ripe eggs through the system. Rejected eggs may be returned to the pseudocoelom through a **ventral bell opening**. Entrance to the variably long uterus is controlled by the selector apparatus and by a posterior **vaginal sphincter**. The **vagina** opens into the **genital pore** which may be terminal or subterminal and which may occasionally be bordered or surrounded by **accessory structures,** such as lips, papillae, or spines.

The **male reproductive system** usually includes two **testes**; species with a single testis are also known, e.g. those in the echinorhynchid family Fessisentidae. The testes are often spheroid-ovoid and arranged in tandem but may also be long and tubular. Monorchid males have been described in a number of species (see Amin, 1975a, 1989; Bullock, 1962). **The sperm ducts** may be enlarged in some species to form a **seminal vesicle**. There are usually four, six, or eight **cement glands** that may be ovoid, pyriform, elongate, tubular, or intestiniform. They are grouped in three categories: 1) a single syncytial structure with giant nuclei (Eoacanthocephala); 2) up to eight pyriform glands each with a giant nucleus (Archiacanthocephala); or 3) spheroid or tubular glands with fragmented nuclei (Palaeacanthocephala). Paired **cement ducts** originate from the cement glands and occasionally fuse to form the **cement reservoir** which opens into the common **genital canal**. Cement gland secretions ultimately form the **copulatory cap** that plugs the female gonopore after copulation. **Saefftigen's pouch**, the eversible **copulatory bursa**, and the **penis** make up the copulatory structures of male acanthocephalans.

The taxonomic treatment and key included in the following sections are based on adult anatomical features outlined above. For a discussion of the anatomy and development of larval stages (acanthor, acanthella, cystacanth), see Amin (1982b) and Schmidt (1985). The broad range of morphological variability and anomalies in attachment and reproductive structures, among others, have been reported infrequently (see Bullock, 1962; Amin, 1975a, 1989).

Natural History

Only adult forms of acanthocephalans inhabit the intestinal tract of all vertebrate groups. They usually live less than one year in their definitive hosts where they often exhibit seasonality in numbers and maturity. In riverine species, new generations are often recruited by hosts in the autumn after ingestion of crustacean inter-

mediate hosts parasitized by cystacanths. Young recruits undergo growth and development and reach peak size and maturity in the spring. Migration to more posterior intestinal locations has been associated with seasonal development and maturation in many riverine species. The short-lived males are less common in spring collections. Reproductive activity increases in winter and spring as evidenced by greater numbers of females with eggs and copulatory caps (cement plugs) during these seasons. In freshwater acanthocephalans whose hosts inhabit large and deep oligotrophic lakes, seasonality in recruitment, development, maturity, and numbers are not evident (see Amin and Burrows [1977] and other references therein). The absence of cyclic fluctuations is related to the lack of pronounced seasonal temperature oscillations that are known to affect recruitment, maturation, and seasonal availability of intermediate hosts. These seasonal aspects of marine acanthocephalans have been rarely investigated and reported.

Eggs are passed with the definitive host's feces and remain free in the environment until ingested by an arthropod intermediate host. The eggs of aquatic acanthocephalns are usually oval to oblong and show a polar prolongation of the middle membrane. Those of terrestial worms are typically oval, thick-shelled, and show no prolongation of the middle membrane. Aquatic intermediate hosts usually consist of Amphipoda, Isopoda, Copepoda, and Ostracoda, whereas terrestial hosts include insects such as Orthoptera and Coleoptera. Ingested eggs (shelled acanthors) develop into young and (later) older acanthellae in the body cavity of the arthropod intermediate host, where they later develop to the larger infective cystacanth stage. In some acanthocephalan species, larval forms induce alteration in the behavior and/or coloration of the intermediate host (in contrast with noninfected arthropods), making the intermediate host much more readily captured and eaten by the definitive host. Adult breeding and egg production appear to be timed to make eggs available to the intermediate host when its populations are seasonally available and well established. This seasonality is often evident in late spring and in summer in riverine species (see Amin et al., 1980).

Aspects of life history outlined above are universal and are shared by other known acanthocephalan species. In a few species, however, an additional paratenic (transport) host occupies a position between the arthropod intermediate host and the vertebrate definitive host (in which acanthocephalans reach sexual maturity and breed). Paratenic hosts become ecologically indispensible for the completion of the life cycle of these acanthocephalans whose hosts have no direct environmental contact with intermediate hosts. Less frequently, a definitive host may become a paratenic host if the infected intermediate host contained larvae that had not yet reached the infective cystacanth stage. In paratenic hosts, immature worms are usually encysted in or on body cavity organs. Transmission of adults from one definitive host to another through predation also is known to occur.

Techniques

The following methods of processing acanthocephalans for whole mounting were originally adapted from Bullock[1]:

1 Remove adults carefully from host intestinal mucosa without injuring or losing any of the parts, particularly the proboscis, which may need to be removed separately. Record worm distribution, pathology, and related observations. Cut intestinal sections with intact worms and clear pathology and preserve in 4% formaldehyde (10% formalin) for future histopathological studies.
2 Refrigerate freshly recovered specimens overnight to extend the proboscis, then fix in refrigerated AFA (alcohol-formalin-acetic acid) or in 75% ethanol if AFA is not available.
3 Prick specimens individually with a fine needle such as an insect mounting pin. Prick large and thick specimens more than once. Do not prick through reproductive or attachment structures.
4 Stain in Mayer's acid carmine overnight.
5 Destain next morning with 4% HCl in 70% ethanol until pink.
6 Rinse three times in 75% ethanol or until no more stain leaches out of specimen.
7 Place 12 to 24 h in 85% ethanol.
8 Place 12 to 24 h in 95% ethanol.
9 Repeat step 8.
10 Place 12 to 24 h in 100% ethanol; longer in large worms.
11 Place 12 to 24 h in 25% terpineol/75% absolute ethanol (by volume).
12 Place 12 to 24 h in 50% terpineol/50% absolute ethanol (by volume).
13 Place 12 to 24 h in 75% terpineol/25% absolute ethanol (by volume).
14 Place 12 to 24 h in 100% terpineol.
15 Place 12 to 24 h in pure terpineol mixed with Canada balsam in equal proportions by volume. Alternative clearing agents: xylene or oil or winter green.
16 Whole mount in Canada balsam.

[1] Bullock, W. L. 1973. 13 Thompson Lane, Durham, NH 03824. Personal. commun.

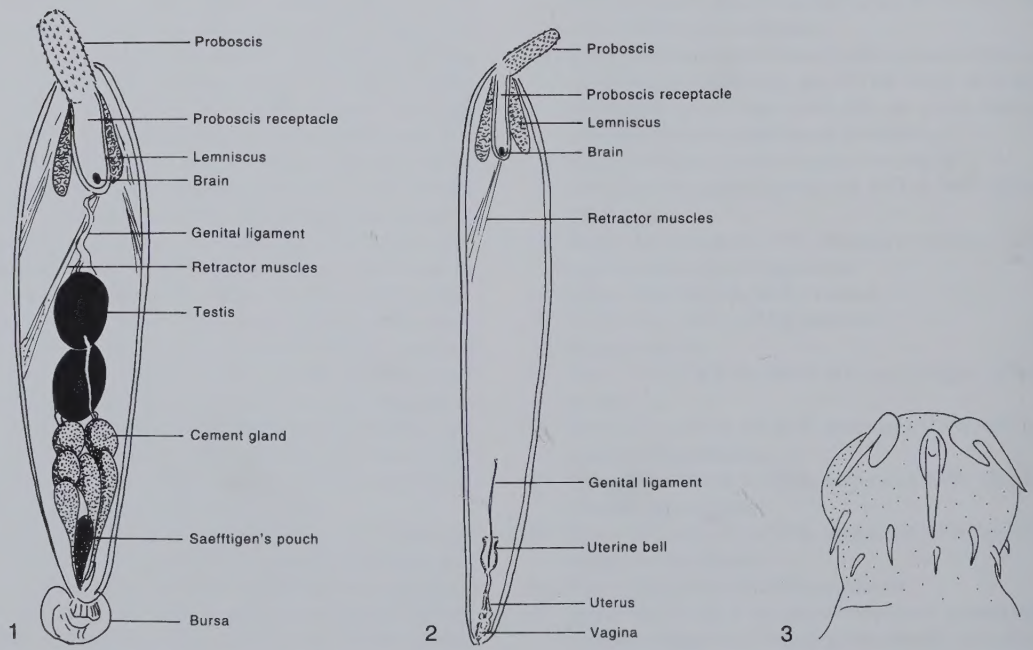
Important notes: Specimens should not be removed from vials or taken out of solution. Change fluids only by withdrawing or adding with uncontaminated Pasteur pipettes. After use, discard all alcohol concentrations. All fluids containing terpineol are reusable. Do not leave solution bottles or specimen vials open longer than absolutely necessary. Air moisture may cause total and irreversible opaqueness in specimens when mounted in balsam. In such cases, returning specimens to the 100% ethanol stage and repeating subsequent steps may save the day.

Key to Genera

The following key includes mostly marine genera known from marine fish and mammals. The key also includes the following categories of acanthocephalans: 1) genera reported from birds captured in Atlantic coastal areas or whose intermediate hosts comprise marine invertebrates; 2) genera utilizing marine invertebrates as paratenic hosts; 3) marine genera (determined from host distribution) from waters of neighboring countries adjacent to the study area covered by this manual; and 4) freshwater genera with occasional records in marine or estuarine hosts. The key is based on the concepts reported by Amin (1987a). Most figures were made with the aid of original descriptions.

1a Main longitudinal lacunar canals lateral. Lemniscal, cement gland, and hypodermal nuclei fragmented. Ligament sacs in females single, not persistent. Proboscis cylindrical to spheroid usually with many hooks in alternating longitudinal rows (Figs. 1, 2). Proboscis receptacle double-walled ..... **Class Palaeacanthocephala** 2

1b Main longitudinal lacunar canals median. Lemniscal, cement gland, and hypodermal nuclei gigantic. Ligament sacs in females double, persistent. Proboscis usually small with few radially arranged hooks (Fig. 3) Proboscis receptacle single-walled ..... **Class Eoacanthocephala, Order Neoechinorhynchida** 8



Figures 1–3

(1) Adult male *Acanthocephalus dirus* from New Hampshire. **(2)** Adult female *Acanthocephalus dirus* from New Hampshire. **(3)** Proboscis of *Neoechinorhynchus cylindratus.*

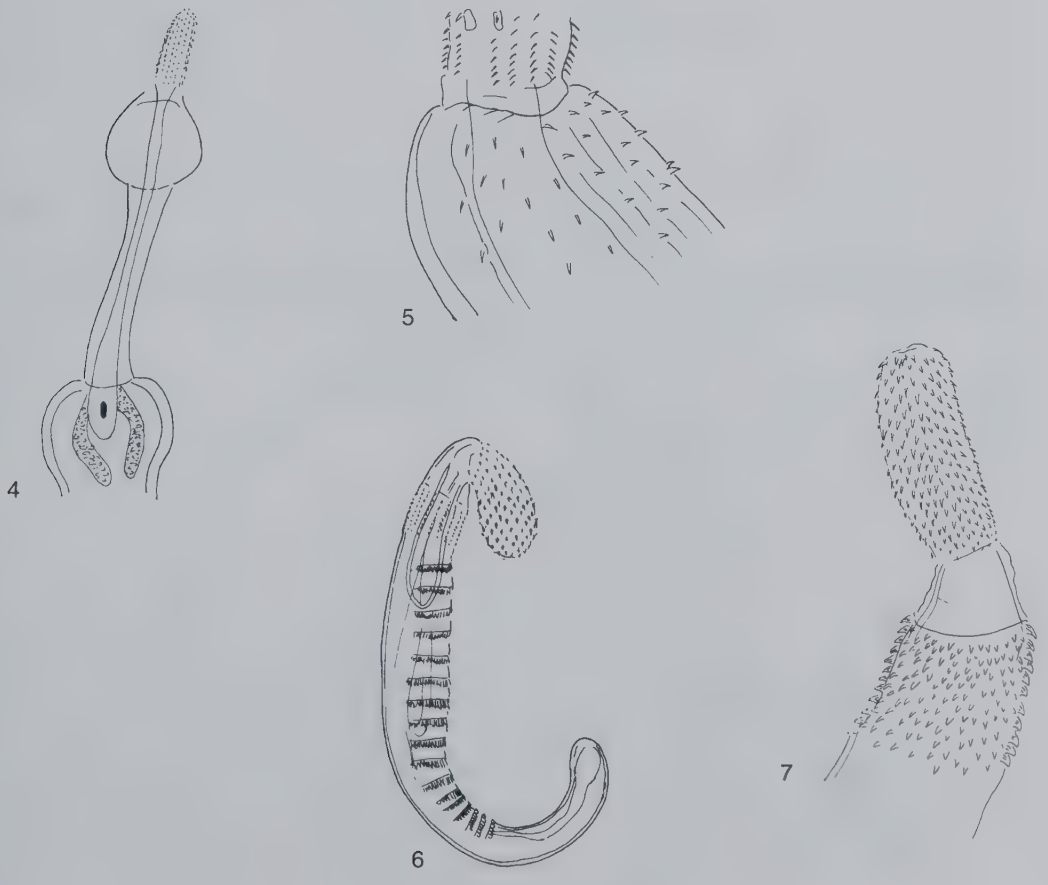
2	Parasites of fishes and amphibians	**Order Echinorhynchida**	**3**
	Parasites of reptiles (rarely), birds, and mammals	**Order Polymorphida, Family Polymorphidae**	**15**

3a Neck very long and cylindrical or spirally twisted with or without bulbous swelling. Proboscis receptacle long and inserted at base of proboscis (Fig. 4). Parasites of freshwater and marine fishes ..... **Family Pomphorhynchidae, Genus *Pomphorhynchus***

3b Neck and proboscis receptacle not long (Figs. 1–3) **4**

4a Trunk usually unarmed (Figs. 1, 2); armed individuals with anterior minute cuticular spines **5**

4b Trunk usually armed (Figs. 5–7); cuticular spines may rarely be replaced by sclerotized plaques or absent. Unarmed worms with dendritic hypodermal nuclei, subcylindrical proboscis, long proboscis receptacle with anterior brain, and 6–8 compact cement glands **6**



Figures 4–7

(4) Anterior trunk, neck, and proboscis of *Pomphorhynchus bulbocolli.* **(5)** Anterior trunk of *Tegorhynchus.* **(6)** Young male *Serrasentis sagittifer.* **(7)** Anterior trunk and proboscis of *Gorgorhynchus medius.*

5a Proboscis cylindrical with many hooks or spheroid with few hooks. Cement glands 6 or 8, usually pyriform to spherical, and compact (Fig. 1). Parasites of freshwater or marine fishes, and occasionally amphibians ..... **Family Echinorhynchidae, Subfamily Echinorhynchinae 9**

5b Proboscis claviform to long and slender. Cement glands 4, elongate, and tubular, or filiform (Fig. 8). Parasites of freshwater and marine fishes ..... **Family Cavisomidae, Genus *Filisoma***

6a Trunk spined in one undivided region anteriorly (Fig. 5) and often at posterior extremity. Cement glands 8, elongate pyriform. Parasites of marine and freshwater fishes ..... **Family Illiosentidae 10**

6b Trunk usually spined differently (Figs. 6–7), rarely unspined. Cement glands 4 or 6, elongate and tubular or short and pyriform; 6 or 8 in some unspined species. Parasites of marine and freshwater fishes ..... **Family Rhadinorhynchidae 7**

7a Trunk with many ventral-transverse combs of spines behind anterior collar of spines (Fig. 6) ..... **Subfamily Serrasentinae, Genus *Serrasentis***

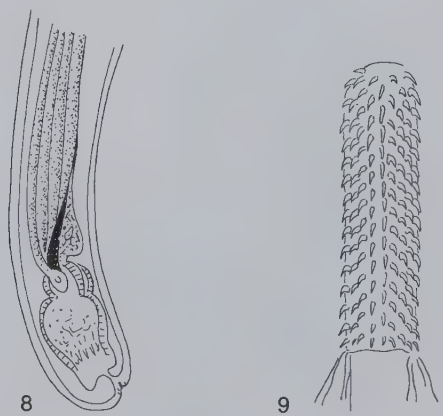
7b Trunk spines in 1 or 2 regions anteriorly (Fig. 7), or infrequently absent or replaced by sclerotized plaques ..... **Subfamily Gorgorhynchinae 11**

8a Proboscis short and subglobular or subcylindrical, armed with a small number of hooks arranged in spiral, circular, or diagonal rows (Fig. 3). Parasites of fishes and amphibians ..... **Family Neoechinorhynchidae 13**

8b Proboscis relatively long and cylindrical, armed with many hooks arranged quincuncially in longitudinal rows (Fig. 9). Parasites of fishes ..... **Family Tenuisentidae Genus *Paratenuisentis***

9a "Brain" at posterior end of proboscis receptacle (Figs. 1, 2) ..... **Genus *Acanthocephalus***

9b "Brain" near middle of proboscis receptacle ..... **Genus *Echinorhynchus***



Figures 8 and 9
(8) Tubular cement glands and posterior end of *Filisoma.* **(9)** Proboscis of *Paratenuisentis ambiguus.*

10a Proboscis ensheathed in a conspicious hyaline membrane (Fig. 10) ..... **Genus *Tegorhynchus***

10b Proboscis without a hyaline membrane (Fig. 11) ..... **Genus *Dollfusentis***

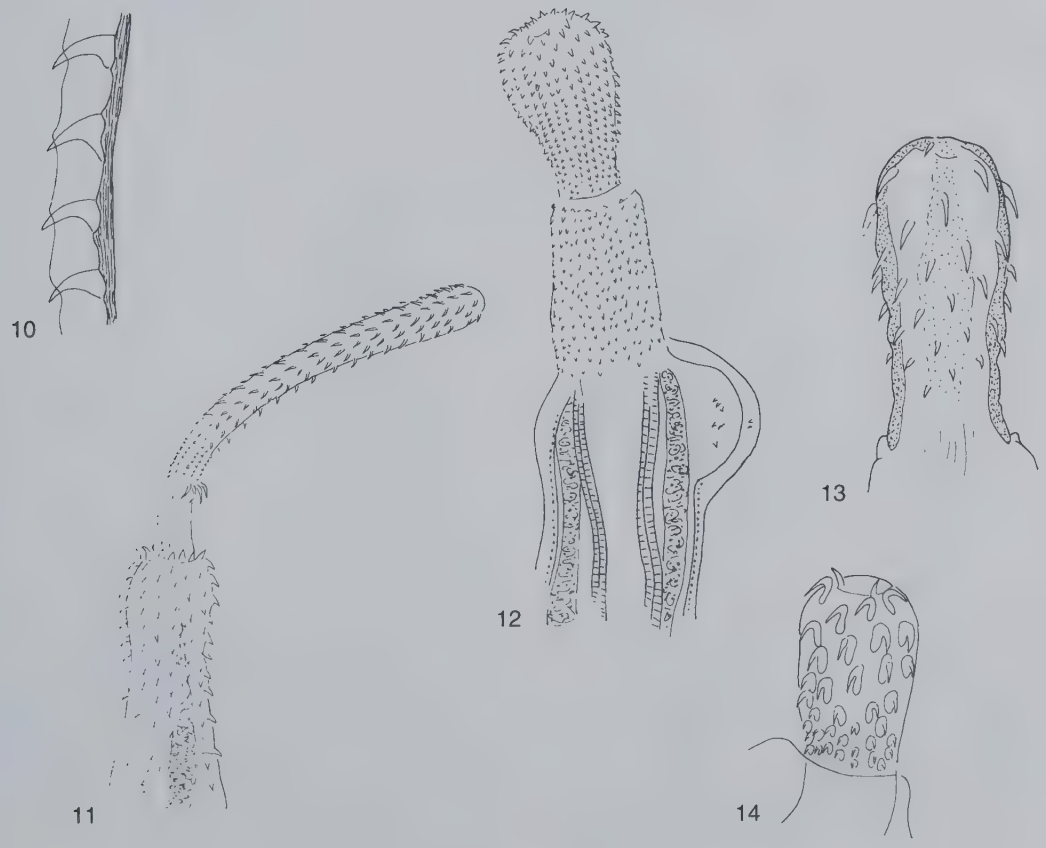
11a Trunk with dorsal bulboid swelling anteriorly (Fig. 12) ..... **Genus *Gorgorhynchoides***
Trunk without bulboid swelling **12**

12a Trunk armed anteriorly with irregularly arranged spines in pits (Fig. 7) ..... **Genus *Gorgorhynchus***

12b Trunk unarmed ..... **Genus *Leptorhynchoides***

13a Proboscis with 3 circles of hooks each with 6 hook (Fig.3) ..... **Genus *Neoechinorhynchus***

13b Proboscis with more hooks (Figs. 13, 14) **14**



Figures 10–14

(10) Proboscis hooks and hyaline sheath of *Tegorhynchus*. **(11)** Anterior trunk and proboscis of *Dollfusentis chandleri*. **(12)** Anterior trunk and proboscis of *Gorgorhynchoides elongatus*. **(13)** Proboscis of *Floridosentis elongatus*. **(14)** Proboscis of *Atactorhynchus verecundus*.

14a Proboscis with 8 diagonal rows of about 7 hooks each (Fig. 13) ..... **Genus *Floridosentis***

14b Proboscis with 8 diagonal rows of about 8 hooks each anteriorly and about 16 smaller hooks posteriorly (Fig. 14) ..... **Genus *Atactorhynchus***

15a Posterior trunk with genital spines in at least one sex (Fig. 15) **16**

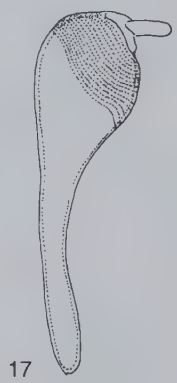
15b No genital spines in either sex **17**

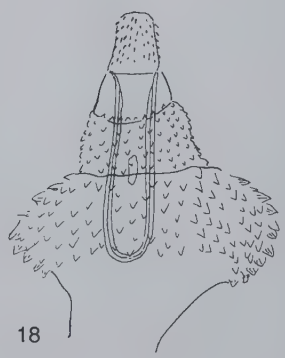
16a Swollen anterior trunk with 2 fields of spines (Fig. 16) ..... **Genus *Andracantha***

16b Swollen anterior trunk with 1 field of spines (Fig.17) ..... **Genus *Corynosoma***

17a Anterior trunk greatly swollen and with 1 field of spines, separated from rest of trunk by narrow constriction (Fig. 18) ..... **Genus *Bolbosoma***

17b Anterior and posterior portions of trunk not separated by constriction, with 1 or 2 fields of trunk spines **18**





Figures 15–19

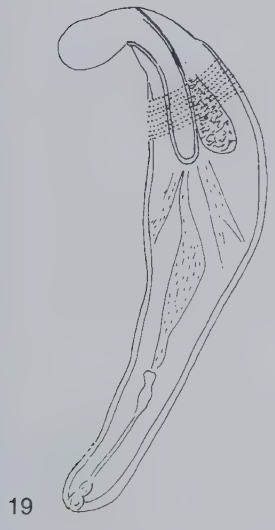
(15) Posterior end of *Andracantha mergi* showing genital spine. **(16)** Female *Andracantha gravida.* **(17)** A female *Corynosoma* sp. **(18)** Anterior trunk and proboscis of *Bolbosoma turbinella.*

18a Two fields of trunk spines in at least one sex (Fig. 19); trunk somewhat short. Four cement glands ..... **Genus *Southwellina***

18b One field of trunk spines (Fig. 18); trunk variable in length, cement glands 2 or 4 ..... **19**

19a Trunk extremely long; 2 or 4 cement glands. Middle of proboscis usually enlarged with greatly enlarged ventral hooks (Fig. 20) ..... **Genus *Arhythmorhynchus***

19b Trunk often short; 4 cement glands. Proboscis cylindrical, ovoid, spindle-, or pear-shaped with no dorso-ventral differentiation or abrupt extreme enlargement of hooks (Figs. 21, 22) ..... **Genus *Polymorphus***



19

20

21

22

Figures 20–22

(19) Female *Southwellina dimorpha.* **(20)** Proboscis of *Arhythmorhynchus uncinatus.* **(21)** Proboscis of *Polymorphus* (*Polymorphus*) *brevis.* **(22)** Proboscis of *Polymorphus* (*Profilicollis*) *altmani.*

Annotated Systematic List

The following list of primarily marine acanthocephalans from the eastern seaboard of the United States is arranged systematically in two palaeacanthocephalan orders (Echinorhynchida [with five families] and Polymorphida [with one family]), and one eoacanthocephalan order (Neoechinorhynchida [with two families]) according to the classification system of Amin (1982a, 1985a). The list includes 43 species in 20 genera, most of which are distributed in marine or estuarine waters along the Atlantic coast of the United States. Orders, families, genera, and species are listed alphabetically under classes Palaeacanthocephala and Eoacanthocephala, irrespective of their marine affinities, hosts, or distribution. Available type and voucher material of the listed species are obtainable from the Biosystematics and National Parasite Collection unit of the Agricultural Research Service, USDA, Beltsville, MD. (J. Ralph Lichtenfels, curator) and from the Harold W. Manter Laboratory, University of Nebraska State Museum (Mary H. Pritchard, curator). Host and distributional data from museum records have been useful in text treatment.

The following text emphasizes host records and geographical distribution. Systematic notes will also be included when relevant but no systematic decisions will be made at this time. Areas where such decisions need to be made will, however, be pointed out for future studies (for synonyms, see Amin, 1985a).

All echinorhynchid and neoechinorhynchid acanthocephalans discussed below are known from marine and estuarine fishes and occasionally from freshwater fishes collected in Atlantic coastal streams of North America. All polymorphid acanthocephalans were taken from birds captured over, in, or near the same geographical regions.

Class PALAEACANTHOCEPHALA Meyer, 1931.
Order ECHINORHYNCHIDA Southwell and McFie, 1935.
Family CAVISOMIDAE Meyer, 1932.

***Filisoma fidum* Van Cleave and Manter, 1947,** was described from Bermuda chub, *Kyphosus sectatrix*, in the Dry Tortugas, Florida. The host genus, *Kyphosus*, is represented on the Atlantic and Pacific coasts of North America by distinct species that might have gradually diversified from common ancestors during isolation (Van Cleave and Manter, 1947). Eight species of the genus *Filisoma* Van Cleave, 1928, are currently recognized and a key distinguishing *F. fidum* from other species in the genus is included in Amin and Nahhas (1994).

Family ECHINORHYNCHIDAE Cobbold, 1876.
The genera *Acanthocephalus* Koelreuther, 1771, and *Echinorhynchus* Zoega in Müller, 1776, are two of the largest echinorhynchid genera with over 45 and 41 species, respectively, reported from freshwater and marine fishes and occasionally from amphibians (Amin, 1982a, 1985a).

***Acanthocephalus dirus* (Van Cleave, 1931) Van Cleave and Townsend, 1936,** is a freshwater species that has been redescribed and documented from 65 species and 16 families of fishes (Amin, 1984). It has three distinct populations: 1) in the Mississippi River drainage system; 2) Wisconsin and Lake Michigan; and 3) the New England states (Amin, 1985b, 1986a; Amin and Huffman, 1984). Its New England population has been reported from 14 species and 9 families of fishes including Atlantic tomcod, *Microgadus tomcod*, and American eel, *Anguilla rostrata*, in the Oyster River, a New Hampshire estuary, downstream from the dam separating it from a freshwater Mill Pond (Bullock, 1962; Bullock[2]). Host and geographical distribution of adults depends on the extent of dispersal of its intermediate host(s) (Amin, 1985b). The intermediate hosts of *Acanthocephalus dirus* are the isopod *Asellus intermedius* (= *Caecidotea militaris* in Wisconsin) in riverine situations and the amphipod *Pontoporeia affinis* in Lake Michigan (Amin, 1978). The ecology of *A. dirus* has been studied in various parts of its range by a number of authors including Seidenberg (1973), Amin (1975b), and Camp and Huizinga (1980), and its larval development by Amin (1982b).

***Echinorhynchus gadi* Zoega in Müller, 1776.** Since its original description, *E. gadi* has been reported from a considerable number of marine and estuarine fish species from Russia; Barents, White, Baltic, and North seas; Gulf of Finland; Scandanavian waters; Sea of Japan; and the Atlantic coast of North America. The large number of host species (see Petrochenko, 1956; Yamaguti, 1963; Valtonen and Crompton, 1990, for partial lists) from diverse families and their wide range of geographical distribution clearly reflects the great degree of morphological variability in this species that is perhaps one of the widest among acanthocephalan species. This variation has contributed to a long list of synonymies describing different populations of *E. gadi* as new species. Van Cleave recognized this fact and cautioned that "Failure to recognize the extreme plasticity of this form has caused many workers to describe as new species forms which on the basis of essential characteristics are wholly indistinguishable from one another." At least 12 synonyms are listed in synonymies (Amin, 1985a). In addition, the subspecies *callariae* Viborg, 1795, and *virentis* Rathke, 1799, are regarded as *E. gadi*; *E. gadi*

[2] Bullock, W. L. 1994. 13 Thompson Lane, Durham, NH 03824. Personal commun.

sensu Van Cleave (1924a) (= *E. vancleavei* Golvan, 1969); *E. gadi* sensu Yamaguti, 1935 (= *E. yamagutii* Golvan, 1969); and *E. gadi* sensu Southwell and MacFie, 1925 (= another species).

Whether *E. gadi* is a species complex is an often asked question. Huffman and Bullock (1975) distinguished with meristogram analysis two "populations" of *E. gadi* obtained from two distinct sets of hosts from the American Atlantic coast. Amin and Redlin (1980) and Shostak et al. (1986) demonstrated that worm age, host species, and geographical location contribute to the morphological variability in taxonomically important characters. The latter authors further showed that meristogram analysis alone is not sufficient to delineate taxa and hypothesized that "geographical variability may be a consequence of restricted gene flow." The taxonomic identity of *E. gadi* is too complex to be realistically resolved within the scope of the present study.

In addition to the definitive hosts (including those from North American Atlantic coast fishes) listed in Petrochenko (1956) and Yamaguti (1963), see lists included in Huffman and Bullock (1975), Meyers (1978), Shostak et al. (1986), Gartner and Zwerner (1989), Arai (1989), Landry et al. (1992), Linton,[3] and museum records. The fish definitive hosts from the Atlantic coast of North America (New Brunswick-Canada, Maine, New Hampshire, New Jersey, Virginia), drawn in part from above sources, include: *Acipenser oxyrhynchus, Alosa aestivalis, A. pseudoharengus, A. sapidissima, Ammodytes hexapterus, Anarhichas lupus, Clupea harengus, Coregonus clupeaformis, Coryphaenoides rupestris, Cymatogaster aggregate, Gadus macrocephalus, G. morhua, G. ogac, Glyptocephalus cynoglossus, Hemilepidotus hemilepidotus, Hemitripterus americanus, Hippoglossoides platessoides, Hippoglossus hippoglossus, Icelinus filamentosus, Leptocottus armatus, Liparis atlanticus, Lycodes cortezianus, Mallotus villosus, Macrourus berglax, Melanogrammus aeglefinus, Merluccius productus, Microgadus proximus, M. tomcod, Morone saxatilis, Myoxocephalus octodecemspinosus, M. polycanthocephalus, M. quadricornis, Nemichthys scolopaceus, Nezumia bairdi, Oncorhynchus gorbuscha, O. keta, O. kisutch, O. nerka, O. tshawytscha, Paralichthys dentatus, Platichthys stellatus, Pleuronectes americanus, P. ferrugineus, Pleuronectes putnami, Podothecus acipenserinus, Pollachius virens, Raja radiata, Reinhardtius hippoglossoides, Salmo salar, Salvelinus alpinus, S. fontinalis, S. malma, S. namaycush, Scophthalmus aquosus, Sebastes aleutianus, S. alutus, S. babcocki, S. borealis, S. caurinus, S. diploproa, S. flavidus, S. helvomaculatus, S. proriger, S. ruberrimus, S. zacentrus, Tautoglabrus adspersus, Theragra chalcogramma, Urophycis chuss, U. tenuis.*

The intermediate hosts of *E. gadi* are amphipods of the genera *Aeginia, Amphithoe, Calliopius, Caprella, Cyphocaris, Gamarellus, Gammarus,* and *Pontoporeia,* and the mysid, *Mysis.* Intermediate hosts known from the North American Atlantic Coast include *Aeginina longicornis, Gamarellus angulosus, Calliopius laeviusculus* (Marcogliese (1994); Bullock[2]).

***Echinorhynchus laurentianus* Ronald, 1957,** was reported in the Gulf of St. Lawrence from marine Heterostomata. These hosts include *Glyptocephalus cynoglossus, Hippoglossoides platessoides, Hippoglossus hippoglossus, Pleuronectes americanus, P. ferrugineus, P. putnami, Reinhardtius hippoglossoides, Scophthalmus aquosus,* and various species of flounders (see Arai, 1989, for a review of these records). Many of these fish hosts also are found in the northern U.S. Atlantic waters. This common distribution probably encompasses shared parasite faunas including *E. laurentianus.*

Family ILLIOSENTIDAE Golvan, 1960.

Genus *dollfusentis* Golvan, 1969, was erected to accommodate a species originally described by Linton (1905) and to relegate three illiosentid species described by Cable and Linderoth (1963) to it. All four species are included in the present review.

***Dollfusentis chandleri* Golvan, 1969** (= *Telosentis tenuicornis* (Linton, 1905) Van Cleave, 1918) has the widest range of host and geographical distribution of all species of *Dollfusentis.* Chandler (1934) provided a detailed emended description of the species from Galveston Bay, Texas. It was later redescribed by Salgado-Maldonado (1976) who also described the fifth species of the genus, *Dollfusentis bravoae* Salgado-Maldonado, 1976, from Cozumel, Quintana, Mexico. This species has been reported from many marine and estuarine localities north and south of the Gulf of Mexico. Southernmost locations extend into Brazil from *Haemulon sciurus* (see Kohn and Macedo, 1984). Its North American range includes the Atlantic Coast of Massachusetts, Maryland, Virginia, North Carolina, Florida, Mississippi, Louisiana, Alabama, and Texas.

Definitive hosts from the above locations include *Acipenser oxyrhynchus, Archosargus probatocephalus, Bairdiella chrysura, Cynoscion arenarius, C. nebulosus, C. regalis, Eucinostomus argenteus, Larimus fasciatus, Leiostomas xanthurus, Lobotes surinamensis, Micropogonias undulatus, Monacanthus hispidus, Morone americana, M. saxatilis, Orthopristis chrysoptera, Paralichthys dentatus, Polydactylus octonemus, Tylosurus acus* and *T. carribaeus.* Sources for the above geographical and host records include Chandler (1934, 1935), Van Cleave (1947), Bullock (1957, 1960), Huizinga and Haley (1962), Yamaguti (1963),

[3] Linton, E. 1933. Notes on Acanthocephala mainly from fishes and birds of the Woods Hole region; submitted to Proc. U.S. Natl. Mus. Wash., D.C., 81 p., 11 pl. Unpubl. manuscr.

Bullock and Mateo (1970), Williams and Gains (1974), Buckner et al. (1978), Overstreet (1978), Jansen and Burreson (1990), Thoney (1991), Linton,[3] and museum records.

O'Rourk (1949), Sogandares-Bernal (1955), Bullock (1957), and Huizinga and Haley (1962) studied prevalences of *D. chandleri* in North Carolina, Louisiana, Texas, and Maryland coastal waters. Amphipod intermediate hosts include *Lepidactylus* sp., *Grandidierella bonnieroides*, and *Corophium lacustra*. These hosts were reported from high and low salinity waters of the coast of Alabama, Mississippi, and Louisiana by Buckner et al. (1978) and Overstreet (1978). Amphipod hosts are usually eaten directly by fish definitive hosts, and paratenic transport hosts are not involved in the life cycle of this acanthocephalan.

***Dollfusentis centrorhynchus* (Cable and Lineroth, 1963) Golvan, 1969,** was originally described from *Mulloidichthys martinicus* in Jamaica by Cable and Linderoth (1963) and later reported from Florida by Bullock and Mateo (1970). No other records of this acanthocephalan were published since.

***Dollfusentis heteracanthus* (Cable and Linderoth, 1963) Golvan, 1969,** was originally described from *Platophrys ocellatus, Gerres cinereus, Bathygobius soporator*, and *Labrisomus nuchipinnis* in Curaçao by Cable and Linderoth (1963) and later reported from Florida by Bullock and Mateo (1970).

***Dollfusentis longispinus* (Cable and Linderoth, 1969) Golvan, 1969,** was originally described from *Anisotremus virginicus* in Jamaica and probably extends into Florida waters. The validity of this species was questioned by Bullock and Mateo (1970). Its suggested synonymy with *D. chandleri* may be validated upon careful study of a long series of specimens and data analysis.

***Tegorhynchus furcatus* (Van Cleave and Lincicome, 1939) Bullock and Mateo, 1970,** was described as *Illiosentis furcatus* from *Menticirrhus americanus* off Grand Isle, Louisiana. It has since been reported from the same host species in coastal Mississippi and Alabama (Overstreet, 1978) and from *Fundulus similis, Dasyatis sabina, D. say*, and *D. americana* off Horn and Ship islands, Mississippi (Buckner et al., 1978). Museum (the Manter Laboratory) data include records of *T. furcatus* from *D. say*, and *Menticirrhus americanus* in the Caribbean, from *Trachinotus carolinus* in Mississippi, from *M. saxatilis* in Massachusetts, and from *Polydactylus octonemus* and *M. americanus* in Texas.

Intermediate hosts of *T. furcatus* include *Lepidactylus* sp. and *Haustorius* sp. Both amphipod genera were reported off Horn Island, Mississippi, where adults were collected from fish definitive hosts (Buckner et al., 1978) as well as from *Lepidactylus* sp. in the northern Gulf of Mexico (Overstreet, 1978).

Family Pomphorhynchidae Yamaguti, 1939.
Genus *pomphorhynchus* Monticelli, 1905, is represented by four species in this review. Two species, *P. rocci* Cordonier and Ward, 1967, and *P. tereticollis* (Rudolphi, 1809) Meyer, 1932, primarily infect marine fishes but also may be found in freshwater coastal fishes. The other two species, *P. bulbocolli* Linkins in Van Cleave, 1919, and *P. lucyi* Williams and Rogers, 1984, are freshwater species that occasionally infect marine or brackish water fishes. The first two species have been very difficult to distinguish by using morphological characteristics or host ecology; see Samuel et al. (1976), Huffman and Nickol (1978), and Gleason and Huffman (1981). Differentiation based on comparative length of proboscis hooks in the 60% to 80% position region and a certain hook ratio appear to have resolved the problem (Gleason and Huffman, 1981).

***Pomphorhynchus bulbocolli* Linkins in Van Cleave, 1919,** is widely distributed in North American freshwater fishes and has been reported from at least 81 host species (Samuel et al., 1976). See Amin (1987b) for a discussion of its ecology and host relationships. Reference is made here to only marine fish hosts of *P. bulbocolli*. Van Cleave (1924a) reported *P. bulbocolli* from *Roccus lineatus* (= *Morone saxatilis*), the type host of *P. rocci*. *Pomphorhynchus bulbocolli* also infected the marine *Microgadus tomcod* and *Fundulus* sp. from the brackish waters directly below the last dam on the Oyster River, New Hampshire (Bullock, in Huffman and Nickol, 1978); infected intermediate hosts may have washed over the dam. *Pomphorhynchus bulbocolli* also was reported from *Anguilla rostrata* in New Hampshire by Muzzall (1981). Overstreet (1978) also reported *P. bulbocolli* from *Amia calva* and other unnamed fishes from low-salinity habitats in the northern Gulf of Mexico.

The intermediate hosts of *P. bulbocolli* include *Hyalella azteca* and *Gammarus pseudolimnaeus* (Amphipoda), and *Caecidotea communis* (Isopoda) (Gleason, 1987, 1989; Muzzall, 1981, 1982). Muzzall (1981) also reported *P. bulbocolli* infections in "estuarine amphipods of the genus *Gammarus*" from New Hampshire. Attempts to infect *H. azteca* with *P. rocci* failed (Johnson, 1973, personal commun. in Samuel et al, 1976) thus lending credibility to the distinctive identity of each of *P. rocci* and *P. bulbocolli*.

***Pomphorhynchus lucyi* Williams and Rogers, 1984,** appears to have little host specificity. It was described from 14 mostly freshwater species of fish belonging to 7 families and 6 orders from northern Florida and south-

ern Alabama. Fish hosts with marine or brackish affinities included Atlantic needlefish, *Strongylura marina*, and American eel, *Anquilla rostrata*. No other reports of *P. lucyi* are published to date.

***Pomphorhynchus rocci* Cardonnier and Ward, 1967,** was described from *Morone saxatilis* off the North Carolina coast. Other marine hosts include *Paralichthys dentatus* and *Merluccius bilinearis* from Raritan Bay, New Jersey (Meyers, 1978) and *Pleuronectes putnami* from Great Bay Estuary, New Hampshire (Burn, 1980). Brackish water records include infections in *Micropterus salmoides* in North Carolina and freshwater records involved *Ictalurus furcatus*, *Pylodictus olivaris*, and *Aplodinotus grunniens* in Louisiana and Mississippi (Huffman and Nickol, 1978). A curious record from *A. grunniens* in a noncoastal freshwater stream, the Ohio River in West Virginia, was reported by Joy et al. (1986). The brackish water marine amphipod *Gammarus tigrinus* is the known crustacean intermediate host of *P. rocci* (see Samuel et al, 1976; Muzzall, 1981).

***Pomphorhynchus tereticollis* (Rudolphi, 1809) Meyer, 1932,** is a Nearctic species that also is reported in Ireland from *Gadus* sp., *Acipenser sturio*, and *Salmo fario*. In North America, it was reported "in great numbers" from *Morone saxatilis* as well as from *Cynoscion regalis* and *Synodus foetens* off Woods Hole, Massachsetts and North Carolina by Linton (1889) as *Echinorhynchus proteus* Westrumb, 1821, and Meyer (1932), respectively.

Family RHADINORHYNCHIDAE Travassos, 1923.
Subfamily GORGORHYNCHINAE Van Cleave and Lincicome, 1940.

Genus *Gorgorhynchoides* Cable and Linderoth, 1963, is distinguished from other rhadinorhynchid genera by an anterior dorsal swelling of the trunk; the swelling may or may not be spined. The description of much of the *Gorgorhynchoides* material by Cable and Mafarachisi (1970) was based on collections by Linton deposited at the USNM Helm. Coll., catalogue nos. 8044, 8045. Cable and Mafarachisi (1970) reported that these specimens were not mentioned in Linton's publications and indicated that they were aware that Linton "intended to erect a new genus and had selected a type male and a type female." They were not aware that he had already described the genus as "*Aulorhynchus* n. gen." (with trumpet snout) in a significant contribution that was not published because of his death (Linton[3]). Linton named his type species "*Aulorhynchus longulus* n. sp.," the description and figures (64–71) of which are very similar to those of *Gorgorhynchoides lintoni* Cable and Mafarachisi, 1970. It was collected from *Seriola lalandi* in 1910 near the Woods Hole region, Massachusetts.

The species of the genus *Gorgorhynchoides*, as emended by Cable and Mafarachisi (1970), are treated independently as valid in this study. The validity of these species is, however, not unquestionable and separate study of their systematic identity is warranted.

***Gorgorhynchoides bullocki* Cable and Mafarachisi, 1970,** was originally collected from *Caranx hippos*, *Lutjanus griseus*, and *Bairdiella chrysura* off the Florida Gulf coast and farther south into Chetumal Bay, Mexico.

***Gorgorhynchoides elongatus* Cable and Linderoth, 1963** (description emended by Cable and Mafarachisi, 1970), was initially collected from *Caranx crysos* in Curaçao but probably extends farther north into the geographical range covered by this study.

***Gorgorhynchoides lintoni* Cable and Mafarachisi, 1970,** was reported from *Caranx crysos*, *Seriola lalandi*, and *Trachinotus falcatus* from the northern Atlantic coast of the United States, see discussion of the genus (above).

Genus *gorgorhynchus* Chandler, 1934, was established to contain *Echinorhynchus medius* Linton, 1908 (whose cement glands were reinterpreted by Chandler, 1934) and to describe *G. gibber* which was considered synonymous with *G. medius* (see Amin, 1985a). Three species of *Gorgorhynchus* are reported here.

***Gorgorhynchus cablei* Golvan, 1969,** was described from *Lutjanus jocu* from Jamaica and is probably present in the southern range of the area covered by this study.

***Gorgorhynchus clavatus* Van Cleave, 1940,** was collected from *Paralabrax humeralis* in the Galapagos and Jamaica and probably extends into the geographical range covered by this study; *Lutjanus* appears to serve as a paratenic host.

***Gorgorhynchus medius* (Linton, 1908) Chandler, 1934** (= *Gorgorhynchus gibber*, Chandler, 1934), was reported from *Arius felis*, *Mycteroperca venenosa*, and *Orthopristis chrysoptera* from the Atlantic coast of Florida and Texas and farther south into the Gulf of Mexico and Bermuda Islands. The species was redescribed from *Arius melanopus* collected in Veracruz, Mexico, by Salgado-Maldonado (1978). Encapsulated immature worms were found "among the viscera . . . of spiny rayed fishes" (Chandler, 1935).

***Leptorhynchoides thecatus* (Linton, 1891) Kostylev, 1924,** is a common parasite found in at least 6 families of freshwater fishes, particularly centrarchids, and extends over a wide geographical range in North America. It is often found encysted in the body cavity of fish

paratenic hosts (see Petrochenko, 1956; Yamaguti, 1963; Hoffman, 1967; and museum records for partial host lists). Its ecology and host associations were reported by Amin (1988) in Wisconsin and by others elsewhere. Its intermediate hosts include amphipods of the genus *Hyalella*. It has been reported from "fresh-brackish water interface" in a "variety of marine intruders" in the northern Gulf of Mexico in Mississippi and Alabama by Overstreet (1978).

Subfamily SERRASENTINAE Petrochenko, 1956.

***Serrasentis sagittifer* (Linton, 1889) Van Cleave, 1923,** is the only species of the genus *Serrasentis* Van Cleave, 1923, that is reported from the study area. It was most completely described by Travassos (1966) and redescribed by Salgado-Maldonado (1978). Synonymies were reported by many authors such as Travassos (1966), Jupta and Jain (1985), Amin (1985a), and Amin et al. (1984). It has been reported from various marine waters in the world including the tropical Atlantic with records extending from Texas and Florida in *Arius felis, Bairdiella chrysura, Paralichthys dentatus, Rachycentron canadum, Cynoscion regalis* to New Jersey in *P. dentatus* and *Pomatomus saltatrix* (see Meyers, 1978; Overstreet, 1978; and museum records). Reservoir (paratenic) hosts in Atlantic North America include *B. chrysura, Centropristis striata, Clupea harengus, Coryphaena hippurus, Lagodon rhomboides, Leiostomus xanthurus, Micropogonias undulatus, Orthopristis chrysoptera, Paralichthys albigutta, Pomatomus saltatrix, Prionotus tribulus, Stenotomus chrysops, Synodus foetens,* and *Gobiomorus fuscus*; and see Linton (1889, 1901, 1905; Overstreet, 1978).

Order NEOECHINORHYNCHIDA Southwell and MacFie, 1925.
Family NEOECHINORHYNCHIDAE Ward, 1917.

Subfamily ATACTORRYNCHINAE Petrochenko, 1956.

***Atactorhynchus verecundus* Chandler, 1935,** was described from *Paralichthys lethostigma* in Galveston Bay, Texas, and subsequently reported from *Cyprinodon variegatus* in other Texas locations (Bullock, 1957), the west coast of Florida (Bullock, 1960), Mobile Bay, Alabama (Williams and Gaines, 1974), Mississippi (Overstreet, 1978), and Long Island, New York (Bullock, 1962). This acanthocephalan species appears to be very host specific to *C. variegatus*.

***Floridosentis elongatus* Ward, 1953,** was described from *Mugil cephalus* in Biscayne Bay, Miami, Florida, and later collected from the same host species in southern Texas (Bullock, 1957) and the the southwestern coast of Florida (Bullock, 1960). It was redescribed from the same host species in Mexico by Salgado-Maldonado and Barquin-Alvarez (1978). Other hosts include *M. Curema* from Puerto Rico (Cable and Quick, 1954) and from Mobile Bay, Alabama (Williams and Gaines, 1974). The same two species of *Mugil* also are reported hosts of *F. elongatus* in the Pacific Ocean, at least off the Mexican coast at La Paz, Baja California, and Mazatlan, Sinaloa (Bravo-Hollis, 1969).

Subfamily NEOECHINORHYNCHINAE Travassos, 1926.

***Neoechinorhynchus doryphorus* Van Cleave and Bangham, 1949,** is a rarely reported species that was originally described from *Jordanella floridae* in the Cape Haze-Englewood area of Florida. The recovery of similar forms from marine waters elsewhere in the world (Amin et al., 1984) suggests that the geographical distribution of *Neoechinorhynchus* forms with unequal proboscis hooks in the anterior circle is considerably wider than previously thought. Extensive collections at least in the Florida estuaries should prove their presence there. Larval stages were recovered from the mesenteries of *Fundulus majalis* (see Van Cleave and Bangham, 1949), *Lucania parva* and *Notropis* sp. in Florida brackish waters at Cape Haze-Englewood (Bullock, 1960).

***Neoechinorhynchus rostratum* Amin and Bullock, 1998.** There are about 18 species of *Neoechinorhynchus* Stiles and Hassall, 1905, that occur in North American freshwater hosts, mostly centrarchids and turtles. The *Neoechinorhynchus* material collected from American eel, *Anguilla rostrata,* along the New England and Canadian coasts is very similar to the freshwater *N. cylindratus* (Van Cleave, 1913) Van Cleave, 1919, but differs in the following features. It has an estuarine geographical distribution in eel, does not occur as adults in the nearby freshwater centrarchids, and has a slightly different morphology of the egg and female posterior end. This new species maintains breeding populations in eel. Adults collected from *Microgadus tomcod* do not reach sexual maturity in this marine-estuarine host. Immature individuals were frequently found in liver and mesenteries of *Fundulus heteroclitus*.

Family TENUISENTIDAE Van Cleave, 1936.

***Paratenuisentis ambiguus* (Van Cleave, 1921) Bullock and Samuel, 1975,** the only species of the genus, was erected for *Tanaorhamphus ambiguus* Van Cleave, 1921, from *Alosa pseudoharengus, Anguilla rostrata, Fundulus diaphanus,* and *Morone americanus*. The natural definitive host is *A. rostrata* from Maryland, Massachusetts, and New Hampshire coastal areas. Unnatural hosts include *Microgadus tomcod* and *Fundulus heteroclitus* from

New Hampshire and *Alosa pseudoharengus*, *Morone americanus*, and *F. diaphanus*. Intermediate hosts include *Gammarus mucronatus* from Maryland and *G. tigrinus* from New Hampshire (Bullock and Samuel, 1975).

Order POLYMOPHIDA Petrochenko, 1956.

Family POLYMORPHIDAE Meyer, 1931.

Six polymorphid genera from birds and mammals represent the only acanthocephalans reported from nonpiscine hosts in this review.

Genus *Andracantha* Schmidt, 1975, was erected for three polymorphid acanthocephalans having genital spines and two fields of trunk spines. Two of these species had been assigned previously to *Corynosoma* Lühe, 1904, and occur within the coastal areas covered by this study. The third species, *Andracantha phalacrocoracis* (Yamaguti, 1939) Schmidt, 1975, is known from the pelagic cormorant, *Phalacrocorax pelagicus*, from Alaska and Japan (Schmidt, 1975) and from the common cormorant, *P. carbo*, in Czechoslovakia (Scholz et al., 1992). Three other species of *Andracantha* are found elsewhere in the world.

***Andracantha gravida* (Alegret, 1941) Schmidt, 1975,** was reported from the double-crested cormorant, *P. auritus floridanus*, and brown pelican, *Pelicanus occidentalis carolinensis*, in Cuba, Florida, and Louisiana (Schmidt, 1975), and the Gulf of Mexico.

***Andracantha mergi* (Lundström, 1941) Schmidt, 1975,** is less host specific than *A. gravida*. It was reported from the red-breasted merganser, *Mergus serrator*, and red-throated loon, *Gavia stellata*, in Alaska; from the lesser scaup duck, *Aythya affinis*, in New York; from the black-crowned night heron, *Nycticorax nycticorax*, in New Hampshire (juvenile worms) (Schmidt, 1975); and from the American bald eagle, *Haliaeetus leucocephalus*, in New Jersey and Nova Scotia (Nickol and Kocan, 1982). Additional hosts include *P. auritus* in Maine and *Pholis gunnellus* (rock eel, paratenic host) in New Brunswick, Canada (museum collections). The original description was based on specimens collected from *M. serrator* in Sweden.

***Arhythmorhynchus uncinatus* (Kaiser, 1893) Lühe, 1912,** was one of three species of Acanthocephala described from unnamed hosts in Florida. It was the "object of conjecture" among taxonomists until it was later more completely described by Van Cleave (1924b) from some of Kaiser's original material. Adults have not been reported since and the definitive host(s) remain unknown. Immature worms were recovered from the mesenteries of a marine fish, sheepshead, *Archosargus probatocephalus*, in Florida by Bullock (1960).

Genus *Bolbosoma* Porta, 1908, includes parasites of whales, and as immature worms, may occasionally infect humans (Beaver et al., 1983; Tada, et al., 1983). Two species are reported here.

***Bolbosoma turbinella* (Diesing, 1851) Porta, 1908,** was primarily reported from the blue whale, *Balaenoptera musculus*, in North American Atlantic waters. It is not, however, restricted to Atlantic blue whales and is also found in the Pacific waters of North America. Other definitive hosts include sei whale, fin whale, humpback whale, North Atlantic right whale, and North Atlantic bottlenose whale (Measures, 1992, 1993). The sei whale and right whale feed mostly on copepods. The fin whale and the humpback whale are euryphagous and feed on swarming fish (Nemato, 1959; Mitchell, 1975). Ten families of fish from various geographical locations include known paratenic hosts of *B. turbinella* (see review by Measures, 1992).

***Bolbosoma vasculosum* (Rudolphi, 1819) Porta, 1908,** has been reported from dolphins, *Delphinus delphis* and *Mesoplodon bidens* in North American Atlantic waters, Mediterranean Sea, and Sea of Japan as well as from the roundnose grenadier, *Coryphaenoides rupestris* in the North Atlantic Ocean (Bakey and Zubchenko, 1984). Fish paratenic hosts from various geographical locations are listed in Petrochenko (1958) and Yamaguti (1963)

***Corynosoma constrictum* Van Cleave, 1918,** was described from American scoter, *Oidemia americana*, in Yellowstone Lake, Wyoming, by Linton (1892) as *Echinorhynchus striatus*. It has since been reported from various species of ducks in inland and coastal North American locations. Hosts include *Anas acuta*, *A. americana*, *A. carolinensis*, *A. clypeata*, *A. discors*, *A. platyrhynchos*, *A. rubripes*, *Anas* spp., *Aythya affinis*, *A. marila*, *Bucephala albeola*, *Cygnus olor*, *C. buccinator*, *Fulica americana*, *Erismatura jamaicensis rubida*, *Melanitta deglandi*, *M. niger*, *Oidemia americana*, *Phalaropus tricolor*, *Podiceps grisegena*, and *Recurvirostrata americana* (see Van Cleave, 1918; Van Cleave and Starrett, 1940; Petrochenko, 1956; Yamaguti, 1963; and museum records). The North American Atlantic distribution is often more northerly, e.g. in New Hampshire, New York, and into Canada in *Anas*, *Aythya*, and *Cygnus*.

***Corynosoma wegeneri* Heinze, 1934,** adults commonly infect gray and ringed seals, *Erignathus barbatus*, *Halichoerus grypus*, *Phoca fasciata*, *P. hispida*, *P. richardi*, and *P. vitulina* from the northwest Atlantic to Greenland.

Paratenic fish hosts include *Gadus morhua, Hemitripterus americanus, Hippoglossoides platessoides, Macrozoarces americanus, Melanogrammus aeglefinus, Myoxocephalus octodecemspinosus, M. scorpius, Osmerus mordax, Pleuronectes americanus, P. ferrugineus,* and *Scophthalmus aquosus* from New Hampshire, Maine, the Canadian New Brunswick and Scotian Shelf, and Greenland (Meyer, 1954; Petrochenko, 1956; Marcogliese and McClelland, 1992; and museum records). Recent increases in *C. wegeneri* populations in ground fish appear to be related to observed marked growth in seal populations (Marcogliese and McClelland, 1992). Similar observations were made on other species of *Corynosoma* of the Antarctic fur seal in South Georgia and South Drkneys by Zdzitowiecki (1987).

Genus *Polymorphus* Lühe, 1911.

The position, concept, and composition of the genus *Polymorphus* were critically evaluated and a new diagnosis of the genus was made based on the designation of *Hexaglandula* Petrochenko, 1950, and *Subcorynosoma* Hoklova, 1967, as junior synonyms (Amin, 1992). Other taxonomic changes were proposed and two subgenera are now recognized: *Polymorphus* Lühe, 1911, with 36 species and *Profilicollis* Meyer, 1931, with 10 species. A key to the species of the genus is included in Amin's (1992) critical revision of this genus.

Eight polymorphic species are recognized from birds whose range includes Atlantic North American coastal areas; four in each of the subgenera *Polymorphus* and *Profilicollis.*

***Polymorphus* (*Polymorphus*) *acutis* Van Cleave and Starrett, 1940,** is a Nearctic species that usually infects ducks, grebe, gull, coot, and godwit in coastal and inland North American and Siberian locations. It was originally described from mallard, *Anas platyrhynchos,* and pintail, *A. acuta,* taken from the Illinois River, Illinois. Other host records include *Anas clypeata, A. strepera, Aythya ferina, A. fuligula, Bucephala clangula, Fulica americana, Larus argentatus, Limosa limosa, Oxyura leucocephala,* and *Podiceps grisegena* (see Petrochenko, 1958; Amin, 1992). For a comprehensive listing of Russian hosts see Hoklova (1978).

***Polymorphus* (*Polymorphus*) *brevis* (Van Cleave, 1916) Travassos, 1926,** is a parasite of osprey, bitterns, and herons in North America. It was originally described as *Arhythmorhynchus brevis* from the bittern *Botaurus lentiginosus* in Baltimore, Maryland. Travassos (1926) assigned the species to the genus *Polymorphus* and Meyer (1932) accepted this assignment. Van Cleave (1945) reassigned it back to *Arhythmorhynchus* and Salgado-Maldonado (1980) redescribed it from *Nycticorax nycticorax* in Michoacan, Mexico. The species is herein recognized in *Polymorphus* (see Amin, 1992, for a detailed discussion).

Definitive hosts from Atlantic coastal states include *N. nycticorax* from New Hampshire and *Ardea herodias* from Louisiana. Other hosts from elsewhere in the United States include *Botaurus virescens, Gavia immer, Pandion haliaetus carolinensis,* and *Pelecanus erythrorhynchos.* Paratenic fish hosts include *Gambusia affinis, Ictalurus nebulosus, Leiostomus xanthurus, Lepomis cyanellus,* and *Menidia beryllina* in Florida and New Hampshire. For host records see Van Cleave (1916, 1945), Petrochenko (1958), Yamaguti (1963), Amin (1992), and museum records.

***Polymorphus* (*Polymorphus*) *obtusus* Van Cleave, 1918,** was described from water turkey, *Anhinga anhinga,* in Florida. It has since been reported from various aquatic birds in coastal states extending north to New York where it was recorded from *Anas platyrhynchos.* Other hosts include *Ardea herodias, Erismatura jamaicensis, Mergus merganser,* and *Phoenicopterus ruber* (see Van Cleave, 1918, 1924a; Petrochenko, 1958; Yamaguti, 1963; Amin, 1992; and museum records).

***Polymorphus* (*Polymorphus*) *trochus* Van Cleave, 1945,** is a common Nearctic parasite of coot, *Fulica americana* (type host) but rarely infects the mallard duck, *Anas platyrhynchos,* and common moorhen, *Gallinula chloropus,* in North America (Priebe, 1952; Podesta and Holmes, 1970; McDonald, 1988). It is not the same as "*Polymorphus trochus*" of Hoklova (1966) which is recovered mostly from ducks, *Anas* spp., in Asia. The latter is probably a new species (Amin, 1992) In North America, *P.* (*P.*) *trochus* was reported from Atlantic coastal states extending from Florida to New York, as well as from other inland states (see above references for more information).

***Polymorphus* (*Profllicollis*) *altmani* (Perry, 1942) Van Cleave, 1947,** is a parasite of surf scoter and sea diving ducks *Melanitta perspicillata* and *M. deglandi* in California but has also been reported from the former species on the North West Atlantic coast off New Brunswick and Newfoundland (Bourgeois and Threlfall, 1982). Directed collections of coastal New England states will probably reveal its presence there.

***Polymorphus* (*Profilicollis*) *botulus* (Van Cleave, 1916) Witenberg, 1932,** was originally described as *Filicollis botulus* from the circumboreal eider duck *Somateria dresseri* in Maine. Schmidt and Kuntz (1967) and Amin (1985a) recognized that species in *Polymorphus* as the type of the subgenus *Profilicollis.* Hoklova (1974) redescribed the species and reinstated it in her family Filicollidae. This placement is not recognized here.

Polymorphus (*P.*) *botulus* was reported from a variety of sea ducks on both coasts of North America as well as from Eurasia. On the North American Atlantic coast, it also infects the Holarctic common eider duck, *S. mollissima,* where its seasonality and host relationships were reported by Bishop and Threlfall (1974). See also Bourgeois and Threlfall (1982), Clark et al. (1958), and Threlfall (1968) for additional geographical records from eider ducks and scoters (*Melanitta perspicillata, M. nigra, M. fusca*) on the North West Atlantic coast. Records from the North American Pacific coast and Eurasia include a wider variety of birds other than eider ducks and scoters. See Yamaguti (1963) and Ching (1989), and others quoted therein, for records of the shore crab intermediate hosts of *P.* (*P.*) *botulus* in these locations.

***Polymorphus* (*Profilicollis*) *kenti* Van Cleave, 1947** (= *Filicollis sphaerocephalus* Harrington and Pillsbury, 1938, and Harrington, 1939) was described from *Larus argentatus smithsonianus* in Kent Island, New Brunswick, Canada. Bullock[3] found acanthocephalans tentatively identified as *P.* (*P.*) *kenti* in the sand crab, *Emerita* sp., from Florida. These specimens are in the Nebraska State Museum, Lincoln, HWML Coll., nos. 33481 and 33482, as "*Polymorphus* sp. ex *Emerita* sp." In 1960, Bullock[2] attempted to collect *P.* (*P.*) *kenti* from 17 Kent Island gulls that did not yield any worms. Absence of worms is not a rare phenomenon. Hosts from which certain acanthocephalans were initially identified occasionally yield no parasites upon examination in the same locality years later. The distribution of *P.* (*P.*) *kenti* is not limited to the east coast. Reish (1950) described it from gulls in Oregon and from the sand crab *Emerita analoga* (in larval form).

***Polymorphus* (*Profilicollis*) *major* Lundström, 1942,** adults were described from goldeneye duck, *Bucephala clangula,* in Sweden and have since been reported from various Scandinavian locations. Schmidt and MacLean (1978) found it in New England coastal locations in other diving ducks including white-winged scoter, *Melanitta deglandii,* lesser scaup, *Aythya affinis,* bufflehead, *Bucephala albeola,* and canavasback, *A. valisineria.* Juvenile *P.* (*P.*) *major* were also found by Schmidt and MacLean (1978) from rock crabs, *Cancer irroratus,* in Maine shore waters.

Genus *Southwellina* Witenberg, 1932, was erected by Witenberg (1932) who designated *Arhythmorhynchus hispidus* Van Cleave, 1925, as its type species. The genus was not seriously recognized by acanthocephalan taxonomists until Schmidt (1973) redefined and resurrected it, and recognized three species in it; two species are included in this treatment.

***Southwellina dimorpha* Schmidt, 1973,** was described from white ibis, *Eudocimus albus,* in Florida. Intermediate hosts include the crayfish *Procambarus clarkii* from Pecan Island, Louisiana (Schmidt, 1973).

***Southwellina hispida* (Van Cleave, 1925) Witenberg, 1932,** was first described from juveniles collected from frogs in Japan. Adults were subsequently described from specimens found in the heron *Nycticorax n. nycticorax* in Japan by Fukui (1929). Synonyms of *S. hispida* include *Arhythmorhynchus duocinctus* Chandler, 1935, which was described from juveniles found in the mesenteries of the southern flounder, *Paralichthys lethostigma,* from Galveston Bay, Texas. Lincicome (1943) subsequently described the same species from *N. nycticorax* from the Bronx Zoo. Additional definitive hosts include *Pelecanus occidentalis* and *Phalacrocorax auritus* from Florida, and paratenic fish hosts include *Menidia beryllina* and *Fundulus grandis* from Florida and Texas (museum records). Meyers (1978) reported additional fish hosts (*Paralichthys dentatus, Pomatomus saltatrix, Cynoscion regalis*) from Raritan Bay, New Jersey. Synonymies of *S. hispida* from *N. nycticorax* and other definitive bird hosts (*Ardea, Egretta, Phalacrocorax*) from Japan, from Primorye and the Crimea (Russia), and from the Galapagos Islands were discussed by Schmidt (1973). This species' broad geographical distribution (Van Cleave, 1940) extends into Europe, e.g. Hungary (Dimitrova, 1991).

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Omar M. Amin received his B.S. in Biology (1959), M.S. in Medical Entomology (1963) from Cairo University, and Ph.D. in Parasitology (1968) from Arizona State University (ASU). He worked at Old Dominion University (1967–69), the Centers for Disease Control (1969–70), and the University of Wisconsin as a Professor of Parasitology and Epidemiology from 1971 until he established the Institute of Parasitic Diseases (IPD) in 1992, currently in Arizona, providing diagnostic and educational services to the medical community for human parasitic diseases. He also is a Research Professor of Parasitology at ASU, pursuing his research activities in wildlife parasitology, particularly in acanthocephalans of fish.

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